

# What determines the number of dominant species in forests?

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**Abstract:** In this work, the difference in number of dominant species in a community on global scale and successional trajectories was analyzed based on the published data. We explained the reasons of these differences using a resource availability hypothesis, proposed in this work, that the distribution of available resource determined the pattern of community dominance. The results showed that on global scale the number of dominant species of community varied across latitudinal forest zone, namely from single-species dominance in boreal and temperate forest to multi-species codominance, even no dominant species in tropical forest. This was consistent with the pattern of resource distribution on global scale. Similarly, in successional trajectories, the number of dominant species gradually radiated from single-species dominance to multi-species codominance, even no dominant species in tropical forest. The changing available resources in trajectories were responsible for this difference. By contrary, a community was often dominated by single species in temperate or boreal forest. This was determined by the low available resource, especially low available water and temperature. In boreal forest, low temperature greatly reduced availability of water and nutrient, which were responsible for the single-species dominance. In addition, the conclusion that high available resources sustained low dominance of community might be deduced, based on the fact that the dominance of community declined with the increasing of species diversity. To sum up, the richer the available resources were, the lower the dominance of community was, and vice versa. The hypothesis that the

resource availability controlled the dominance of community could well elucidate the difference of community dominance on global and community scale.

**Keywords:** codominance; resource availability; single dominance

## Introduction

The dominance of forest in the horizontal zonation, mainly including boreal forest, temperate forest and tropical forest, decreases gradually from dominance by single species to codominance by several species, even no dominant species. What does this dominance of forest result from? Does the dominance of forest change with habitat? According to Keel and Prance (1979), dominance increased as a function of stress, while Jacobs (1987) hold that in tropical forests dominance by single species often suggested the forest was destroyed before. Usually, the single-species dominated forest occurred in the early successional stage of tropical forest (Yu et al. 1994; Huang et al. 2002). However, disturbance may not be a sole reason for single species dominance (Swamy et al. 2000). Richards (1952) suggested that adverse climatic conditions also sometimes resulted in single species dominance. Actually, disturbance and climatic conditions only locally interpret the dominance. In boreal or temperate forest, climax community is dominated by single species intensively. Also the climatic conditions can't elucidate the essence of dominance because that although tropical forest has excellent moisture and temperature conditions, huge spatial structure, abundant organisms, and high biomass, the soil nutrient store is low (Ceccon et al. 2003), so the destruction of the forest and removal of the above-ground vegetation will permit the loss of the limited soil nutrient reserves by erosion and leaching, and on the adverse condition only one species can dominate community (Fang and Peng 1995). In order to explain dominance of forest community, we put forward available resource hypothesis that the dominance of forest community depends on available resource. We believe that to some extent the disturbance and climatic conditions control available resource (mainly including light, temperature, water, and soil nutrients) which is responsible for the difference of community dominance. The aim of this paper is: (1) to view the trend or difference of community dominance on different scale;

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(2) to validate available resource hypothesis.

## Materials and methods

### Data collection

Data on community dominance are collected from former published literature. The relative important value (RIV) of a species may be a critical indicator to illustrate the importance of the species in the forests. In order to compare RIV from different researches, the references with the same RIV calculation equation ( $\text{RIV} = \text{sum of (relative density + relative frequency + relative dominance)} \times 100 / 3$ ) were selected for analysis. RIV of first dominant species, which represents the codominance or single-dominance to a large degree, was selected for analyses.

### Data analysis

Forest dominance trend or difference on global and community scale was analyzed. Pearson correlation and hierarchical cluster analyses were conducted to analyze the relationship between RIV of first dominant species and tree species number. Statistical significance for analyses was set at  $p < 0.05$ . The above analyses were obtained by the SPSS statistical software package version 15.0.

## Results

### Community dominance pattern in latitudinal forest zone

According to the former researches, in north hemisphere the dominance of climax community varies across the different forest zone. RIV of first dominant species in successional climax of community is approximately 5–20% in tropical forest (Swamy et al. 2000; La Torre-Cuadros and Islebe 2003; Ramanujam and Cyril 2003; Small et al. 2004), 30–50% in temperate forest (Cheng et al. 1999), and over 60% in boreal forest. In climax community of tropical forest, there is multi-species codominance or no prominent dominant species under rich resource conditions. In temperate forest single species dominance is often observed, but codominance is infrequent. The climax vegetation in boreal forest zone is mostly dominated by spruce and pine, and moreover the dominance of community is the most prominent among all forest zones (Jasinski and Angelstam 2002; Lehtonen et al. 2004).

### Dominance pattern in successional communities

After disturbance such as over-logging and storm, the dominance of community varies with the proceeding of succession. In tropical forest, few tree species occur in the early stage of succession, and sometimes only one species can dominate the forest. After the primary forest being logged or burned, soil becomes dry and poor. *Pinus latteri*, which is a light-demanded pioneer species,

will adapt to this adverse environment and gradually develops to pure forest, which could last steady for 100 years (Huang et al. 2002). With the proceeding of succession, the single species dominance of early stage of successional trajectories will be replaced by two or more species and the RIV of first dominant species declines gradually. For example, in *Dacrydium pierrei*-*Xanthophyllum hainanense*-*Syzygium araiocladum* community, which is in the mid-stage of succession, *D. pierrei* retreats gradually from the dominant species group because of the poor regeneration ability, while the moderate-demanded species such as *X. hainanense*, *S. araiocladum*, and *Cryptocarya chinensis* will codominate the community (Yu et al. 1994). Across the successional trajectories the dominance of community in tropical forest declines gradually, from single species dominance to multi-species codominance, even no dominant species (Finegan 1996). However, in temperate or boreal forest the process of succession is simple and lacks of species replacement following disturbance (Carleton and Maycock 1978). Often the forest is dominated exclusively by pine or spruce in the successional trajectories (Harper et al. 2002; 2003).

### Relationship between species diversity and RIV of first dominant species

Based on plenty of researches in all forest zones, we selected 60 groups of datum determined by the number of tree species and the RIV of first dominant species (Table 1). Correlation analysis (Table 1) shows that there is negatively significant correlation ( $n=60$ ,  $r=-0.517$ ,  $p < 0.001$ ) between them. Peltzer et al. (2000) conformed from dominance-diversity curves that lower diversity in forest was in line with lower evenness. Cluster analysis (Fig. 1) shows that the 60 groups' data is obviously classified into four clusters based on RIV of first dominant species and tree species number. For example, the data with the lowest RIV of first dominant species and the most tree species number, including code 3, 39, 35 and 54, have merged into one cluster.

## Discussion

### On global scale

Along the latitudinal zone from equator to arctic pole, the rainfall and quantity of heat decrease gradually. The annual precipitation is about 1 500–4 000 mm, 500–1 000 mm, and less than 500 mm in tropical forest zone, temperate zone, and boreal zone, respectively (Wirth et al. 2002). The mean annual air temperature also shows the same trend as rainfall, about 20–25°C in tropical forest, 5–15°C in temperate zone, and often below 0°C in boreal forest. Soils also are greatly important to plant regeneration and growth. The soil nutrient and organic matter in tropical forest are the lowest because of the fast turnover rate of soil nutrient and organic matter. Therefore, the soil is relatively poor in tropical forest, but soil nutrient can be fully assimilated to supply for the growth and regeneration of plant. By contrary, in boreal forest zone, extreme cold and a short summer growing season are its

predominant environmental features. Low air and soil temperature impose clear limits on the regeneration and growth of trees, and are an important determinant of the rate at which biological processes occur (Henttonen et al. 1986). Excess moisture and consequent oxygen-deficient and extreme low temperature conditions are a major cause of slow mineralization of nutrient and thick accumulation of organic matter in boreal forest (Prescott et al. 2000). So the available nutrient absorbed by plant in boreal forest is very low. This pattern of available resource on global scale determines the distribution of climax community dominance represented, to great extent, by the RIV of first dominant species of community from tropical forest to boreal forest, namely the dominance of climax community is more and more prominent

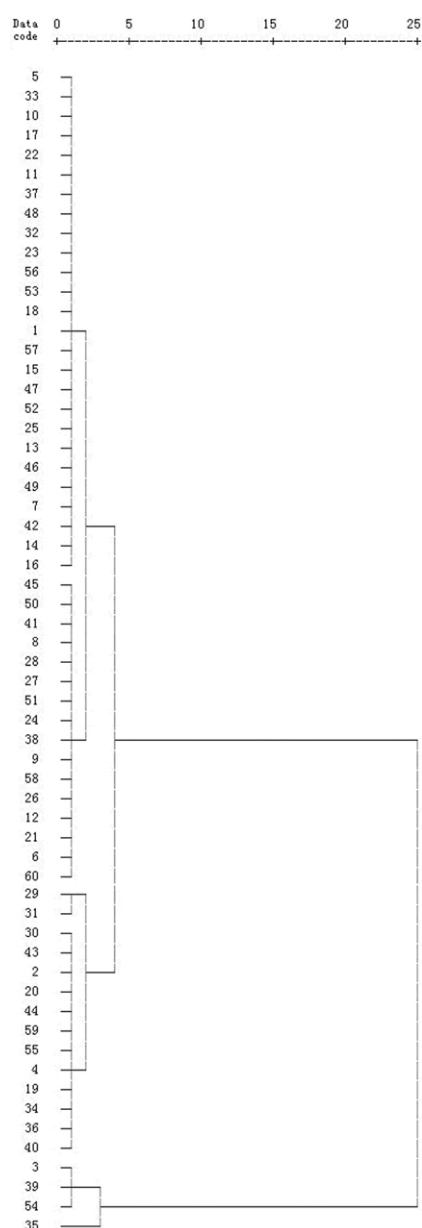


Fig. 1 Hierarchical cluster analysis for the 60 groups' data in Table 1.

### Successional trajectories

Large and short-term disturbance such as over-logging, fire, flood, and storm, can remove the biomass aboveground and degrade the soil. In tropical forest, large disturbance such as extensive logging, extensive tree-fall by storm, flood, and fire, often occur. With the elimination of the plant biomass, firstly, disturbance can induce the degradation of habitat and the losing of topsoil and especially intensify the leanness of soil because of washing by high precipitation which is the dominant pathway for nutrient loss. And then directly hitting the bare ground surface by rainfall can disperse the soil structures into finer particles, which then clog the soil pores. Fire, which is a destructive calamity, can release most of mineral nutrients in the plant biomass for return to the soil, where they become readily available for plant growth. Burning also converts litter and humus of low pH to ash of higher pH which encourages nitrogen-fixing bacteria to produce more nitrogen and these processes improve the soil fertility, while this benefit may not last long. Most of the nutrients will soon be washed away by subsequent rains. Thus, the burning of vegetation will greatly reduce the availability of nutrients in the ecosystem and increase the incidence and intensity of flash floods as well as accelerating soil erosion and siltation. Moreover, disturbance can damage the soil fungal flora that help roots of plant species absorb nutrients from the soil and litter. Large disturbances greatly decrease resource availability in ecological communities (Davis and Moritz 2001). Low available resource, especially soil nutrient and water, can't favor the regeneration of most tree species, and only few tree species can adapt to this adverse habitat. Moreover, low available resource can increase competition among tree seedling or sapling, and then can induce the contabescence of tree species with low competitive ability. Thus, competition gives advantage to species differentiation, which makes one or several species dominate the community. For example, after intensive destruction the forest is often dominated by pine or beech for decades (Fang and Peng 1995). The development of community can improve itself resource availability. Along successional trajectories, pioneer species constantly add organic matter and nitrogen to soil and the ameliorated soil provides a suitable environment for later successional species of vegetation. A high rate of litterfall in restored forests helps restore soil by circulating more nutrients that, to great extent, tune up the regeneration of tree species (Lugo et al. 2004). Organic matter accumulation also alters the conditions in the root zone of the vegetation and influences the species composition. The development of community and litter accumulation can improve the light heterogeneity for seed germination and plant growth. Litter accumulation also can increase soil water which is necessary to tree seed germination and nutrient cycling. The resource availability gradually increases with the proceeding of succession. High nutrient availability can reduce the competitive ability of some plants. High nutrient and weak competitive ability give great chance to the codominance of multi-species. The temporal pattern of resource availability positively restricts community dominance from single species dominance to

codominance by several species along successional trajectories in tropical forest. Similarly, during retrogressive succession the community dominance becomes more and more conspicuous,

which is positively restricted by the declining resource availability, especially soil nutrient availability (Adema and Grootjans 2003; Bardgett 2001).

**Table 1. Relative important value (RIV) of first dominant species (FDS) and the number of tree species (NTS) of community based on different researches**

Data code	FDS	RIV of FDS	NTS	References	Data code	FDS	RIV of FDS	NTS	References
1	<i>Aglaiia elaeagnoidea</i>	25.80	15	Ramanujam and Cyril 2003	31	<i>Diospyros hainanensis</i>	9.27	87	Yang et al. 1994
2	<i>Agrostistachys meeboldii</i>	21.60	53	Swamy et al. 2000	32	<i>Eurya nitida</i>	20.34	13	Ma et al. 2002
3	<i>Altingia obovata</i>	4.72	164	Fu and Feng 1995	33	<i>E. nitida</i>	19.42	18	Ma et al. 2002
4	<i>Beilschmiedia robusta</i>	21.27	69	Li et al. 2005	34	<i>Haematoxylum cam- pechianum</i>	27.80	65	La Torre-Cuadros and Islebe 2003
5	<i>Castanea henryi</i>	18.89	18	Ma et al. 2002	35	<i>Heritiera parvifolia</i>	10.20	136	Yang et al. 1994
6	<i>Castanopsis carlesii</i>	62.12	36	Zhang et al. 1999	36	<i>Hopea parviflora</i>	34.60	74	Swamy et al. 2000
7	<i>C. carlesii</i>	33.10	17	Hong et al. 1999	37	<i>Lepisanthes tetraphylla</i>	17.40	18	Ramanujam and Cyril 2003
8	<i>C. carlesii</i>	45.90	8	Hong et al. 1999	38	<i>Lithocarpus glaber</i>	53.30	7	Hong et al. 1999
9	<i>C. carlesii</i>	53.00	10	He et al. 1998	39	<i>Mallolus hookerianus</i>	4.99	171	Fang et al. 2004
10	<i>C. carlesii</i>	20.38	19	Yan et al. 2002b	40	<i>Manilkara zapota</i>	10.10	68	La Torre-Cuadros and Islebe 2003
11	<i>C. eyrei</i>	22.30	17	Chen 1997	41	<i>Pinus latteri</i>	61.60	20	Huang et al. 2002
12	<i>C. eyrei</i>	48.90	31	Hong et al. 1999	42	<i>Phoebe bournei</i>	34.70	18	He et al. 1998
13	<i>C. eyrei</i>	35.40	11	He et al. 1998	43	<i>Podocarpus imbricatus</i>	22.52	42	Yang et al. 1994
14	<i>C. eyrei</i>	38.00	15	He et al. 1998	44	<i>P. imbricatus</i>	16.30	52	Yang et al. 1994
15	<i>C. eyrei</i>	29.60	16	He et al. 1998	45	<i>Quercus aliena</i> var. <i>acute-serrata</i>	65.90	13	Cheng et al. 1999
16	<i>C. fargesii</i>	37.70	17	Hong et al. 1999	46	<i>Q. glandulifera</i> var. <i>bre-vipetiolata</i>	36.50	9	Cheng et al. 1999
17	<i>C. fargesii</i>	22.15	20	Ma et al. 2002	47	<i>Q. glandulifera</i> var. <i>bre-vipetiolata</i>	31.90	14	Cheng et al. 1999
18	<i>C. fargesii</i>	8.16	25	Su et al. 1995	48	<i>Q. serrata</i>	15.64	19	Ma et al. 2002
19	<i>C. hystrix</i>	22.98	74	Li et al. 2005	49	<i>Q. serrata</i>	39.00	11	Cheng and Xiao 2000
20	<i>C. microcarpa</i>	19.30	57	Shi and Zhu 2003	50	<i>Q. variabilis</i>	63.25	15	Cheng et al. 1999
21	<i>C. platyacantha</i>	39.25	24	Yang et al. 1994	51	<i>Schima superba</i>	42.70	3	He et al. 1998
22	<i>C. platyacantha</i>	21.10	20	Bao et al. 2000	52	<i>Symplocos laurina</i>	32.19	11	Ma et al. 2002
23	<i>C. platyacantha</i>	13.90	22	Bao et al. 2000	53	<i>S. sumuntia</i>	11.80	20	Yan et al. 2002a
24	<i>C. tibetana</i>	52.80	6	He et al. 1998	54	<i>Syzygium araiocladum</i>	11.40	192	Yu et al. 1994
25	<i>Cunninghamia lanceo-lata</i>	29.61	8	Ma et al. 2002	55	<i>Terminalia paniculata</i>	33.30	48	Swamy et al. 2000
26	<i>C. lanceolata</i>	51.22	17	Ma et al. 2002	56	<i>Ternstroemia gymnanthera</i>	13.10	22	He et al. 1998
27	<i>C. lanceolata</i>	39.22	5	Ma et al. 2002	57	<i>Ulmus lamellosa</i>	26.60	12	Bi et al. 2003
28	<i>Cyclobalanopsis chungii</i>	48.00	8	Hong et al. 1999	58	<i>U. lamellosa</i>	58.70	6	Bi et al. 2003
29	<i>Dacrydium pierrei</i>	16.99	93	Yang et al. 1994	59	<i>Vatica astrotricha</i>	19.17	62	Yang et al. 1994
30	<i>D. pierrei</i>	15.10	45	Yang et al. 1994	60	<i>V. mangachapoi</i>	49.89	44	Lan et al. 2007

Note: The area of community selected from former published literature  $\geq$  community minimal area.

The long-term and standing disturbance also can seriously destroy vegetation and topsoil, and then the soil nutrient, which is the limiting factor for plant growth in tropical forest, can't be recruited. These disturbances will lead to the changes of local forest community structure. The research of Ramanujam and Cyril (2003) indicated that the dominance of sacred groves community in anthropogenic stands were more prominent than that in natural forest. Swamy et al. (2000) also reported that repeated burning and other associated disturbances altered the course of succession by giving an advantage to certain species over others such as *Terminalia paniculata* which was single dominant species in its community.

Plant growth is strongly constrained by temperature and precipitation. In temperate or boreal forest, low precipitation and

temperature are major limiting factors for plant growth across the successional trajectories, and the available resource is still poor. Water availability is important for shaping forest structure and composition (Bugmann 2001). Syrjänen et al. (1994) reported that dry sites in natural boreal forest were almost exclusively occupied by *Pinus sylvestris* while on moist sites *Betula* sp. and *Populus tremula* codominated. Low available resource increases the competition, and single dominance of species mainly results from this competitive displacement of other tree species. Only in site with rich resource, there is codominance by two species before succession climax. Similarly, low temperature limits the temporal distribution of tree species on seasonal scale, so a few species can grow under low temperature. Low temperature limits absorbance of water and nutrient across the successional trajec-

tories, so single species often dominates the community, especially in boreal forest. In natural communities soil conditions may determine species composition. Nitrogen is a limiting resource in many temperate forests and nitrogen-fixing plants are usually limited to the early stages of post-disturbance succession. In early stage, the growth and metabolism of nitrogen-fixing plant are very slow, and the organic and inorganic nitrogen in soil are low. Thus, slow nitrogen accumulation limits plant regeneration. Therefore, the single-species dominant community in temperate forests is widely distributed. Regardless that the habitat is dominated by one species or co-dominated by two species in early stage of succession, succession will converge to single species dominance in temperate or boreal forest (Emborg 1998).

#### Deduction from community dominance and species diversity

Low nutrient availability can in part result in low productivity. Resource availability and distribution are important determinants of local plant species diversity (Huston 1994). It is well known that high available resource can sustain high diversity. Based on the fact that the dominance of community declines with the increasing of species diversity on global or successional scale, we can deduce that high available resource may make the dominance of community decline, and vice versa.

#### Conclusion

Both the climatic conditions on the global scale and the disturbance on the local scale can not perfectly explain the essence of dominance. All the difference of dominance of community can be well elucidated by the difference of available resources on the fine scale, namely the resource availability limits the dominance of community. The richer the available resources are, the lower the dominance of community is. The dominance of different community is constrained by different single resource or the combination of several resources. The growth of single species is constrained by the ability of the species within community to acquire resources. Which species to be dominant also depends on the bio-ecological characteristics (such as reproductive ability, pollination ways, seed diffusion ways, maximal height, survival ability of seed and seedling, etc.) and some physi-ecological characteristics, including light-demand, shade-tolerance, low-temperature-tolerance, drought-tolerance, leanness-tolerance, high photosynthesis rate, etc. Sporadically, some stochastic events also can influence the dominance of species. In tropical forest, the member of the dominant species group in climax community isn't unchangeable, even if in the same forest type of similar habitat. The floristic composition of dominant species group can be slightly changed due to certain stochastic events. But the number of species in the dominant species group is still positively constrained by the resource availability. In temperate or boreal forest, the structure and composition are influenced less by chance, but more by competition. The community is intensively dominated by single and relatively fixed species (such as pine, spruce and beech, etc) under poor available resource (Na-

kashizuka 2001). To sum up, the richer the available resources are, the lower the dominance of community is, and vice versa.

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